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The effect of migration on the spatial structure of intraguild predation in metapopulations☆

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Abstract

We consider the effects of migration on intraguild predation (IGP) via lattice models and pair approximation. The following results can be found: there exists asymmetry between two consumers' migration effects on the spatial structure of IGP; migration of each consumer reduces its own clumping degree; the spatial structure is influenced by the ecological neighborhood.

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1. Introduction

Intraguild predation (IGP) has received considerable attention in recent years, as this phenomenon is widespread and therefore has important implications for diversity maintenance in the fields of community ecology, spatial ecology and biological control [1]. IGP is a specific type of predator–prey relationship where the two species also compete for other habitat resources (hereafter, the predator and prey will specifically indicate the intraguild predator and prey) [2]. In cases where the prey is superior at exploiting the shared resource, an equilibrium may be reached and the predator and the prey will co-exist successfully [3,4].

Migration has been observed to be an important factor for predator–prey interactions in ecological communities [5]. One important consequence is that migrations among species based at different trophic positions will show asymmetric effects on the stability and the spatial structure of predator–prey systems [5,6]. Interestingly, Wilson et al. [6] found that the movement of prey has a stronger effect on stability than that of predators. Amarasekare [7] also argued that migration can alter the possibility of coexistence and affect the two consumers' abundance–productivity

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relationships. However, we find that most studies on the effect of migration on the spatial structure are related to simple predator–prey interactions while little is known about that of IGP systems, which are characterized by simultaneous competition and predation. Therefore, a study of the impact of migration on the spatial structure of IGP is required.

Based on a metapopulation framework, we will use two models, pair approximation [8–11] and a cellular automaton model [2,11] to study the above issue. Pair approximation is a useful analysis tool for spatially explicit simulations, which was first used in statistical physics [8,9], and then for ecological researches [10,11]. Furthermore, to express the spatial structure of the predator and the prey, we will adopt the spatial autocorrelation index, join-count statistics (JCS) which was first introduced by Tainaka and colleagues in modelling research [9,12,13]. Here, the spatial intraguild predation model with the addition of terms representing migration will be presented based on metapopulation frameworks and simulation models. The spatial structure for various migration conditions and habitat connectivity will be examined using differential equations and spatially explicit simulations.

2. Models and methods

We consider IGP based on the classical metapopulation framework, i.e. patch occupancy model [14], noting that the mortality of prey can be caused by either local extinction or predation. This is a simple extension of "competitive lottery" models as developed by Chesson and Warner [15]. The above assumptions can be expressed in mathematical terms as follows: define p_+ as the proportion of patches occupied by prey; p_- is the proportion of patches occupied by predator; c_+, c_- are colonization rates of prey and predator; e_+ and e_- are extinction rates of prey and predator, respectively; α is the predation rate. The dynamics of IGP in metapopulation structure then reads:

$$\begin{cases} \dfrac{\mathrm{d}p_+}{\mathrm{d}t} = c_+ p_+ (1 - p_+ - p_-) - e_+ p_+ - \alpha p_+ p_- \\ \dfrac{\mathrm{d}p_-}{\mathrm{d}t} = c_- p_- (1 - p_+ - p_-) - e_- p_- + \alpha p_+ p_-. \end{cases} \tag{1}$$

The model is under the mean-field assumption, which means that all patches are equally connected to other patches, it is often a good approximation for a metapopulation at stochastic steady-states even if migration is distance-dependent [16]. Using invasion analysis [2,17], we can obtain that: (1) the prey can invade when rare (i.e. its per capita growth rate at low density is positive) if $\alpha < (c_+e_- - c_-e_+)/(c_- - e_-)$; (2) the predator can invade when rare if $\alpha > (c_+e_- - c_-e_+)/(c_+ - e_+)$. When the invasion criteria are both satisfied, then the prey and the predator can coexist.

Although this mean-field model is at the heart of many ecological theories, it ignores local ecological interactions. Ecological interactions such as predation, competition and migration processes often occur at spatial scales much smaller than that of the whole population [18]. Pair approximation considers the local ecological interactions available and has been applied successfully to models for a wide range of phenomena [18]. Furthermore, pair approximation is conceptually and mathematically similar to the JCS, which considers the correlations between and within focal species [9,11].

Based on the pair approximation, the dynamics of IGP metapopulations was given by the following set of equations for singlet and doublet probabilities:

$$\frac{\mathrm{d}p_+}{\mathrm{d}t} = \left(c_+ q_{0/+} - e_+ - \alpha q_{-/+}\right) p_+ \tag{2a}$$

$$\frac{\mathrm{d}p_-}{\mathrm{d}t} = \left(c_- q_{0/-} - e_- + \alpha q_{+/-}\right) p_- \tag{2b}$$

$$\begin{aligned} \frac{\mathrm{d}p_{++}}{\mathrm{d}t} &= 2\left[c_+ \frac{1 + (z-1)\, q_{+/0+}}{z} + m_+ \left(1 - \frac{1}{z}\right) q_{+/0+}\right] p_{+0} - 2e_+ p_{++} \\ &\quad - 2m_+ \left(1 - \frac{1}{z}\right) q_{0/++} p_{++} - 2\alpha \left(1 - \frac{1}{z}\right) q_{-/++} p_{++} \end{aligned} \tag{2c}$$

$$\begin{aligned} \frac{\mathrm{d}p_{--}}{\mathrm{d}t} &= 2\left[c_- \frac{1 + (z-1)\, q_{-/0-}}{z} + m_- \left(1 - \frac{1}{z}\right) q_{-/0-}\right] p_{-0} - 2e_- p_{--} \\ &\quad - 2m_- \left(1 - \frac{1}{z}\right) q_{0/--} p_{--} + 2\alpha \left(\frac{1 + (z-1)\, q_{-/+-}}{z}\right) p_{+-} \end{aligned} \tag{2d}$$

Table 1
Probabilities of status transition of patches in the lattice model

Reaction process	Change of status	Transition probability
Birth	$0 \to 1$	$c_+ \sum[p_t(i,j)=1]/z$
	$0 \to 2$	$c_- \sum[p_t(i,j)=2]/z$
Death	$1 \to 0$	e_+
	$2 \to 0$	e_-
Predation	$1 \to 2$	$\alpha \sum[p_t(i,j)=2]/z$
Migration	$0-1 \to 1-0$	m_+/z
	$0-2 \to 2-0$	m_-/z

$p_t(i,j)$ with value 0 (empty), 1 (prey) and 2 (predator) denotes the status of patch (i,j) at time t, and $\sum[p_t(i,j)]$ is the sum of the probability values in the neighbors, e.g. in the lattice network with von Neumann neighborhood, $\sum[p_t(i,j)] = p_t(i+1,j) + p_t(i-1,j) + p_t(i,j+1) + p_t(i,j-1)$. The meanings of other parameters are the same as pair approximation (Eq. (2)).

$$\begin{aligned}\frac{\mathrm{d}p_{+-}}{\mathrm{d}t} &= (c_- + m_-)\left(1-\frac{1}{z}\right)p_{+0}q_{-/0+} + (c_+ + m_+)\left(1-\frac{1}{z}\right)p_{-0}q_{+/0-} \\ &\quad + \alpha\left(1-\frac{1}{z}\right)q_{-/++}p_{++} - (e_+ + e_-)\,p_{+-} - \alpha\frac{1+(z-1)\,q_{-/+-}}{z}p_{+-} \\ &\quad - m_+\left(1-\frac{1}{z}\right)q_{0/+-}p_{+-} - m_-\left(1-\frac{1}{z}\right)q_{0/-+}p_{+-} \end{aligned} \tag{2e}$$

where global density p_σ, with $\sigma \in \{+,-,0\}$, is the probability that a randomly chosen patch is in state σ; doublet density $p_{\sigma\sigma'}$ is the probability that a randomly chosen pair of nearest neighbour patches are in state $\sigma\sigma'$, $\sigma' \in \{+,-,0\}$; local density $q_{\sigma/\sigma'}$ is the conditional probability that a randomly chosen nearest neighbour of a patch in state σ' is state σ; $q_{\sigma/\sigma'\sigma''}$, with $\sigma'' \in \{+,-,0\}$, is the conditional probability that a randomly chosen neighbour of the σ' patch in a $\sigma'\sigma''$ pair patches is in state σ. c_+, c_-, e_+, e_- and α have the same meaning with the mean-field model; m_+, m_- represent the migration rates of the prey and the predator, respectively; z is the ecological neighbourhood which represents the number of neighbouring patches where the range of colonization and migration processes can happen. Noting the definition of pair approximation, we have the following set of relations:

$$\sum_{\sigma\in\{+,-,0\}} p_\sigma = 1 \quad \text{and} \quad \sum_{\sigma\in\{+,-,0\}} q_{\sigma/\sigma'} = 1$$

for any $\sigma' \in \{+,-,0\}$, and also $p_{\sigma\sigma'} = p_\sigma q_{\sigma'/\sigma} = p_{\sigma'\sigma} = p_{\sigma'} q_{\sigma/\sigma'}$, $q_{\sigma/\sigma'\sigma''} \approx q_{\sigma/\sigma'}$. Therefore, the above five probabilities in Eq. (2) are sufficient to calculate all the other singlet and doublet probabilities.

A lattice model was also constructed in order to investigate the spatial structure of IGP. All the patches are arranged on a lattice network of 50×50 patches with synchronous updating (square lattice with von Neumann neighbourhood, $z = 4$; hexagonal lattice with $z = 6$). The periodic boundary condition is adopted, which means that the patch network is like a torus for the two-dimensional lattice [11]. Here, we also allow the migration of individuals, modelled as a random exchange of states between nearest neighbours [5,18,19]. Initially, the two species (prey, predator) are distributed randomly on the lattice network, where each patch is either empty (0) or occupied by prey (1) or predator (2). The initial distributions have little effect on the ultimate behaviour because the system reaches a stationary state, irrespective of initial conditions [5]. Each simulation was run for 1000 steps and the status of each patch changes at most once in each step. The transition probability of status in the patch from time t to $t+1$ is given in Table 1. Although these stochastic simulations are only run discretely for a finite time step, they maintain the essential behaviour of the differential equation model based on pair approximation (Eq. (2)).

JCS can be used to classify quantitatively the distribution patterns as spatially aggregated, segregated or random in terms of the global and local densities used in pair approximation [9,11–13]. Clustering behaviour of species is well described by the spatial clumping degree I_σ, which is defined by $I_\sigma = q_{\sigma/\sigma}/p_\sigma$ in model analysis. In the case of aggregation distribution, we have $I_\sigma > 1$, which indicates the positive first-order spatial correlation between two adjacent occupied patches. The spatially random distribution has $I_\sigma = 1$, which means that the two adjacent occupied patches are independent. The case $I_\sigma < 1$ implies that the spatial distribution pattern is segregated and there exists a negative spatial correlation between two adjacent patches [16]. The degree of species association can also be described

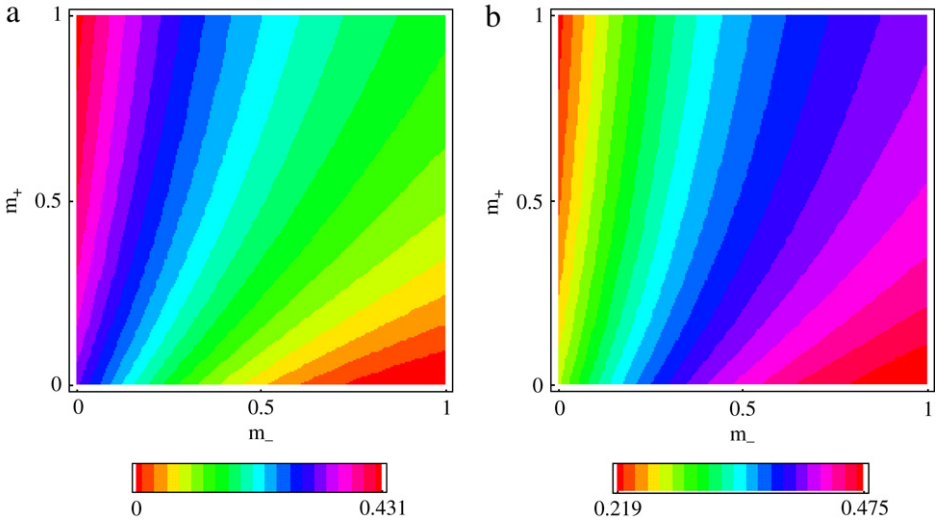

Fig. 1. Influence of prey's migration rate (m_+) and predator's migration rate (m_-) on the global densities of intraguild preys (p_+, (a)) and predators (p_-, (b)). Parameter values are: $c_+ = 0.7$, $c_- = 0.4$, $e_+ = 0.2$, $e_- = 0.2$, $\alpha = 0.25$, $z = 4$.

using JCS [11,20]. Here, we use $A_{\sigma/\sigma'} = q_{\sigma/\sigma'}/q_{\sigma'/\sigma'}$ as the index of spatial association. If $A_{\sigma/\sigma'} > 1$, the species σ' is positively associated with the species σ, i.e. there are more σ populations neighbouring σ' populations than σ' itself. Obviously, $A_{\sigma/\sigma'} < 1$ implies that there exists a negative association and $A_{\sigma/\sigma'} = 1$ means that no association is found. The spatial structure of the predator and the prey will be depicted using indices I_σ and $A_{\sigma/\sigma'}$.

3. Results

Using pair approximation, we can study the impact of migration rates on the global density (p_σ), spatial clumping degree (I_σ) and spatial association ($A_{\sigma/\sigma'}$). One notable result is the asymmetry between the migration effects of prey and predator on the spatial structure of IGP (Figs. 1 and 2). Firstly, the migration rate of predator dramatically affects both the occupancies of prey and predator, while the migration rate of prey only weakly affects the two occupancies (Fig. 1a, b). Specifically, for the prey, the global density p_+ decreases significantly with the migration rate of predator but increases slightly with its own migration rate. However, the predator's global density p_- increases with its own migration rate but decreases slightly with the migration rate of prey. Secondly, we found that the spatial clumping degree I_+ increases with the predator's migration rate (m_-) (Fig. 2a), while I_- does not show a clear pattern as the prey's migration rate (m_+) increases (Fig. 2b). Migration rates of prey and predator also reduce their own spatial clumping degree (I_σ) (Fig. 2a, b). Finally, the response of the spatial association $A_{\sigma/\sigma'}$ also indicates that the migration rate of the predator has a stronger effect on IGP dynamics than that of the prey (Fig. 2c, d), in particular, $A_{-/+}$ can increase from a low value (<1) to one and then to a high value (>1) as m_- increases (Fig. 2c). This indicates that when we increase the predator's migration rate, the spatial association $A_{-/+}$ can change from a negative association to no association and then to a positive association.

In order to clearly exhibit the effect of the neighbouring structure on the dynamics, we plotted the system (2) for different neighbours (Fig. 3) and for comparison, the mean-field assumption was also plotted ($z = +\infty$). The key point to note here is that the spatial structure of metapopulations is influenced by the number of neighbouring patches (z). The global density of the prey (p_+) declines dramatically with the increase of neighbourhood number, yet the global density of the predator (p_-) increases significantly as the neighbourhood number increases (Fig. 3a). This result indicates that high connectivity of habitat patches will benefit the predator, but impede the prey. We also verified that the global densities (p_σ), predicted from pair approximation with the increasing of z, converge to those of the mean-field assumption. This result also implies that the mean-field approximation might overestimate the predator's density and underestimate that of the prey when z is low. The spatial clumping degrees of prey and predator are illustrated, respectively, with different neighbours in Fig. 3b. The clumping degree of prey (I_+) increases sharply as the number of

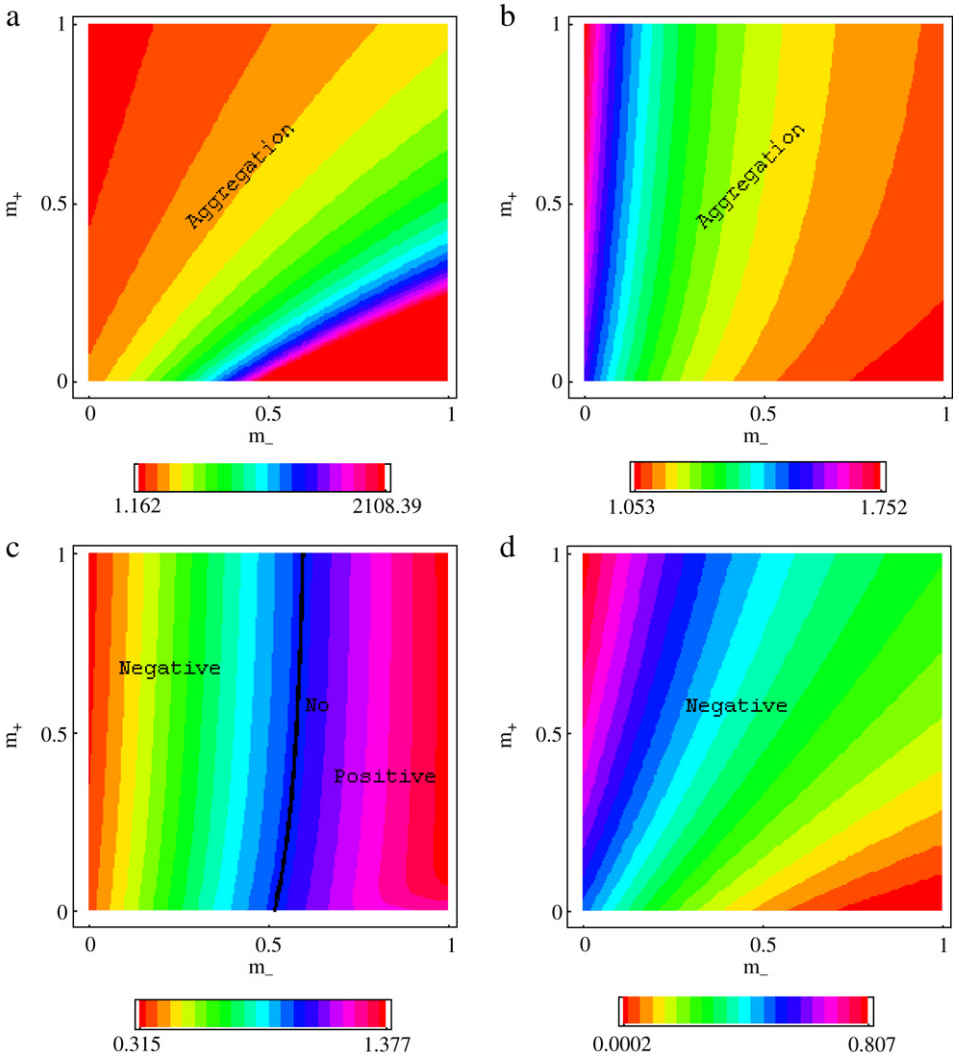

Fig. 2. Influence of prey's migration rate (m_+) and predator's migration rate (m_-) on the spatial clumping degrees of the prey (I_+, (a)) and the predator (I_-, (b)), and on the spatial association between the prey ($A_{-/+}$, (c)) and the predator ($A_{+/-}$, (d)). Note: in Fig. 2(a), (b), the term "Aggregation" means $I_\sigma > 1$; in Fig. 2(c), (d), the terms "Negative", "No" and "Positive" represent $A_{\sigma/\sigma'} < 1, = 1$ and > 1 respectively. Parameter values are the same as in Fig. 1.

neighbours (z) goes from small to medium and then moderately declines as the number of neighbours becomes greater (Fig. 3b). The initial increase of the clumping degree in prey with a small number of neighbours may be because the global densities of both species are more sensitive to a small number of neighbours (Fig. 3a) and the prey shows more clumping behavior to reduce the additional probability due to predation, while, as z increases, the clumping degree of the predator (I_-) constantly decreases (Fig. 3b). The spatial association ($A_{\sigma/\sigma'}$) indicates the attraction of σ' consumers to σ consumers. With the increase of z, the association $A_{-/+}$ increases from a value less than one to a value above one, indicating that more predators will be found around the prey if we improve the connectivity of the patches (Fig. 3c). On the contrary, the association $A_{+/-}$ shows a slight decline with the increase of z (Fig. 3c).

Simulation models show the typical spatial pattern in a stationary state with a hexagonal lattice network under different migration conditions (Fig. 4). From the spatial patterns, we find p_+ is lower when both the predator and the prey migrate ($m_+ = 0.5, m_- = 0.5$) than when there is no migration ($m_+ = 0, m_- = 0$). The above result is consistent with the ones obtained from pair approximation. To compare the results between pair approximation and cellular automaton, we plotted the temporal dynamics of global densities, spatial clumping degrees and associations

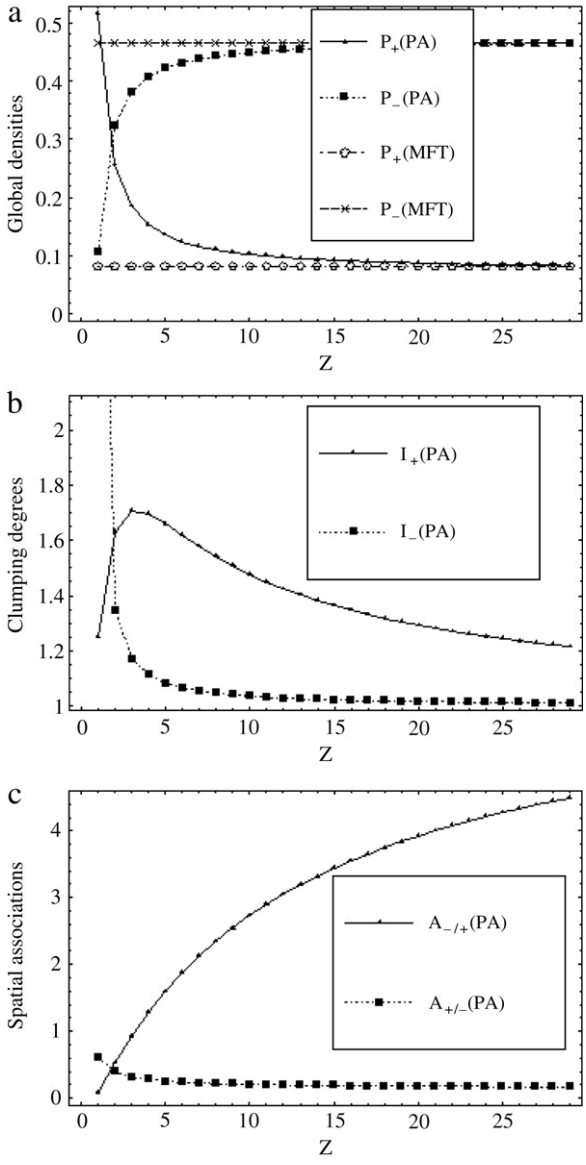

Fig. 3. The effect of ecological neighbourhood (z) on global densities of (p_+, p_-), the spatial clumping degrees (I_+, I_-) and the spatial associations between the intraguild prey and the predator ($A_{-/+}$, $A_{+/-}$). Other parameter values are: $c_+ = 0.7, c_- = 0.4, e_+ = 0.2, e_- = 0.2, \alpha = 0.25, m_+ = 0.5, m_- = 0.5$.

from the two models in Fig. 5. These time series showed that the pair approximation almost captures the same qualitative characteristics as stochastic simulation, but differences still exist between the results. For example, pair approximation does well in predicting the temporal dynamics of the association $A_{+/-}$ (Fig. 5c), but performs poorly in predicting the spatial clumping degree I_+ (Fig. 5b).

4. Discussion

One of the key results is that asymmetry exists between the effects of the prey's and the predator's migrations on the spatial structure of IGP. The predator's migration has more significant effects on the IGP dynamics (those described by p_σ, I_σ, $A_{\sigma/\sigma'}$) than the prey's migration. This difference arose because the two species were engaged in a local competition interaction as well as a local antagonistic (predation) process [7]. The prey has to balance the

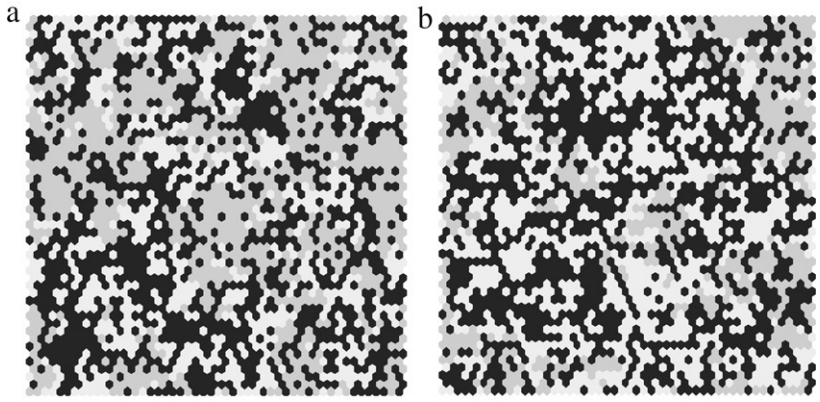

Fig. 4. Two typical spatial distribution patterns of spatial IGP system in hexagonal lattice network (50 × 50 patches). Grey patches are occupied by the intraguild prey; white patches indicate predators and black represent empty patches. Parameters: (a) $m_+ = 0, m_- = 0$; (b) $m_+ = 0.5, m_- = 0.5$. Other parameter values are the same as in Fig. 1.

beneficial influence from its individual's migration with the detrimental impact from predation, which explains why the effect of the prey's migration is not significant on the spatial structure of IGP system. However, the predator's migration creates more opportunities for the predator to contact the prey, and is then beneficial for preying upon the prey. As a consequence, the density of prey decreases markedly with the migration of predators. Note that in Amarasekare [7], results showed that the intraguild predator's migration has affected significantly the intraguild prey's abundance, but the predator's abundance is unaffected by its own migration or that of the prey. However, the spatially local interaction factor in our model has concluded that the occupancy and spatial structures of predators are not only affected significantly by their migration but also slightly by the prey's migration.

The decline in the number of neighbouring patches indicates the drop of patch connectivity, which markedly reduces the abilities for colonization, predation and migration, so the decrease of the number of neighbours will have the same effect as habitat loss [21]. Our results show that an increasing number of neighbours can favour intraguild predators, but impede their prey. The biological reason for this phenomenon could be as follows: as patch connectivity increases, the effective predation effort can be enhanced but the protection from local competition of the prey is weakened, which leads to the result that the density of the prey declines but that of the predator is increased. The results also imply that an intraguild predator is more vulnerable to habitat patch isolation than its prey, which is consistent with previous results which showed that higher trophic levels suffer more from habitat destruction [22].

Our results from JCS show that the spatial clumping degrees of both the intraguild prey and the predator will decline in response to the increase of their own migration rates. Meanwhile, we found that ecological neighbourhood can also effectively influence the spatial structure of IGP system. In fact, these results are common in the natural world [19]. Studies also show that the clumping degree of intraguild prey grows clearly, following the increase of predator's migration rate, which verifies the supposition that the prey population might have the intention to assemble together to reduce the risk of predation. All the results presented in this paper are only a starting point for understanding the importance of migration and its influences on the spatial structure of multi-trophic communities, which definitely merit further exploitation. We also found that there exist substantial differences between results predicted from pair approximation and simulations, therefore improving the power of pair approximation in multi-trophic communities is another important sphere of future research.

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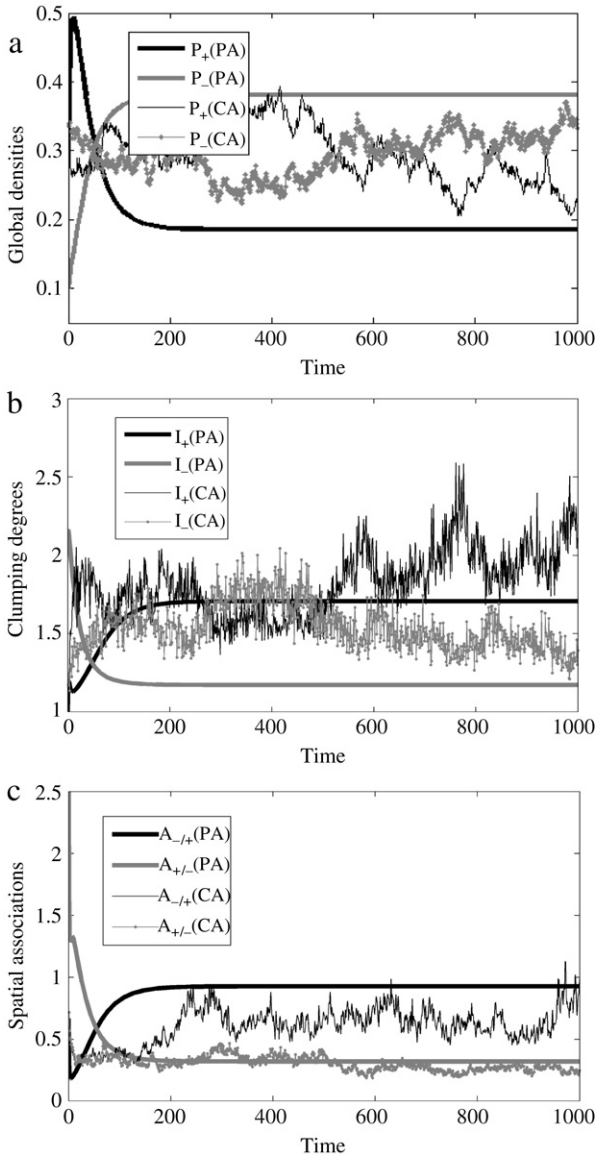

Fig. 5. Temporal dynamics of the global densities (a), spatial clumping degrees (b), and spatial associations (c) under the pair approximation (PA) and the spatially explicit simulation model (cellular automaton, CA, 50 × 50 patches). Parameter values are: $c_+ = 0.7$, $c_- = 0.4$, $e_+ = 0.2$, $e_- = 0.2$, $\alpha = 0.25$, $m_+ = 0.5$, $m_- = 0.5$, $z = 4$.

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